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ON REGENERATION BY EARTHWORMS OF A SPECIES OF THE LUMBRICID GENUS *DENDROBAENA* EISEN 1874.

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Regeneration, either cephalic or caudal, after natural or experimental amputation, for any species of *Dendrobaena* has not been recorded hitherto, though several of the head regenerates attributed by Morgan to *Eisenia foetida* (cf. Gates, 1953, 1954) probably were *D. octaedra*. Some data as to regeneration in another species of the genus can now be presented.

The worms, presumably all of an athecal morph frequently called *Bimastos tenuis* in the past, were clitellate and were secured early in the summer in Michigan. Amputation was without anesthesia. Amputees were kept in damp leaves at 22° C for the periods indicated in the tables.

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Anterior regeneration in *D. rubida* (Savigny, 1826)

All regenerates (cf. Table I) are hypomeric. Metamerism in most regenerates deviates more or less from normal. Regeneration of a head clearly is possible at all levels back to and including 13/14. The regenerate at 17/18 lacks normal anal or buccal sculpturing distally and, since nephropores are unrecognizable, provides no external indications as to whether it is of cephalic or caudal organization.

Abnormal metamerism and hypomery at anterior levels, in certain other earthworm species studied by the author, resulted from unfavorable conditions either in the external or internal environments. Accordingly, metamerically normal regenerates at

all levels to 13/14 and equimery at least to 5/6 can be expected in *D. rubida* when conditions are more favorable.

The level at which the indeterminate monstrosity was developed is close to, if not actually in, a region where regenerative capacity in *E. foetida* (cf. Gates, 1949-1950) is bipotential. Monstrosities such as the one under consideration often are produced in morphogenetic regions of dual capacity. However, the data now available as to the results of posterior amputation in *D. rubida* scarcely warrant anticipation of heteromorphic tail regeneration in that species. Presumably then, a regenerate developing at 17/18 in optimal conditions will be normally cephalic.

Especially noteworthy, even in these few instances, is absence of any indication of decline in number of segments regenerated as level of amputation moves posteriorly (cf. Gates, 1949, p. 137).

TABLE I

Head regeneration in *Dendrobaena rubida*

Serial number	Level of regeneration	Segments in regenerate	Stage of regenerate	Days of regeneration	Remarks
1	2/3	1	2	19	
2	3/4	1	3	19	Metamerism still indistinct in regenerated left halves of iv-vi.
3	5/6	3	4	32	Regenerate metamerism nearly normal.
4	5/6	4	4	32	Regenerate metamerism nearly normal but 6/7 abnormal in regenerated right halves of vi-vii.
5	6/7	3	4	32	Metamerism nearly normal.
6	6/7	4	–3	19	Metamerism probably was developing abnormally.
7	7/8	2	4	37	Metamerism not quite normal. Regenerated ventral half of viii abnormal.
8	7/8	3	3	19	

Serial number	Level of regeneration	Segments in regenerate	Stage of regenerate	Days of regeneration	Remarks
9	7/8	3+	3	19	Proximal portion of regenerate too short for a normal segment.
10	8/9	4	3	19	Metamerism apparently developing abnormally in regenerated right halves of ix-x.
11	8/9	4	4	32	Regenerate segments ii-iv not quite normal.
12	8/9	4	4	32	Segment iv too large. Excised dorsal half of ix had been regenerated.
13	8/9	4	–3	19	Metamerism apparently normal.
14	11/12	5?	4	32	Regenerate metamerism abnormal.
15	13/14	5?	–3	32	Metamerism in regenerated left halves of xiv-xvi probably developing abnormally.
16	13/14	5-6?	–3	30	Metamerism rather indistinct in regenerated portions of xiv-xv, ventral half of xiv and a small portion of xv.
17	17/18	4-6?	–3	32	Regenerate terminating distally in rounded knob like a rudimentary prostomium but towards the ventral rather than the dorsal side.

Except as indicated otherwise above, excisions appear to have been transverse and along intersegmental furrows.

Stages. 1. Prostomium and buccal invagination as yet unrecognizable.
2. Prostomium and mouth developed.
3. Intersegmental furrows demarcate regenerate into segments.
–3. Furrows still indistinct.
4. Pigment present but obviously different from that of substrate.
5. Setae and nephropores recognizable.
6. Pigment now like that of substrate, external stigmata of regeneration, except for typical metameric anomalies, unrecognizable.

Posterior regeneration in *D. rubida*

An anus of more or less normal appearance had been acquired, at end of a July-August period of nineteen days, by the six worms from which a posterior portion of the intestinal region (cf. Table II) had been excised. Healing probably had been enteroparietal. The new anal region had not yet been delimited from the last substrate segment, by development of an intersegmental furrow, in Nos. 4-6 where little or no indication of reorganization is externally recognizable. A very small anal region, in No. 2, is demarcated by an intersegmental furrow and again there are no other external indications of reorganization.

A terminal portion of No. 1, presumably comprising only the last segment, at time of preservation was being reorganized. Completion of the process apparently under way probably would have resulted in development anteriorly of eight new setal follicles with setae and appearance of an intersegmental furrow demarcating a terminal anal portion from a metamere with the usual stigmata of regeneration. Reorganization, instead of regeneration, would then have been recognizable externally only if the original nephropores had been retained in the smaller daughter segment or if some of the pigment had escaped lysis.

Reorganization, accordingly, had been most drastic and had taken place most rapidly at the anteriormost level of amputation.

Evidence as to tail regeneration has been sought in several hundred individuals of *D. rubida* that have been available from various states and from other countries. Many of these worms certainly are posterior amputees and some of the others, obviously brevicaudate, very probably are. No tail regenerates were found. Externally recognizable indications of reorganization were noted but rarely, and in each case there could have been produced, in addition to the anal region, only one or two new segments.

Homomorphic tail regeneration, from a growth zone of rapid segment production (Gates, 1948) obviously does not, usually, follow posterior amputation in this species.

TABLE II

Results of posterior amputation in *D. rubida*

Serial number	Level of amputation	Number of excised segments	Remarks
1	42/43	?	Terminal substrate segment has lost much pigment, setae and nephropores.
2	54/55	?	An intersegmental furrow delimits small white anal region from last substrate segment.
3	65/66	12	Same as in No. 2.
4	80/81	6	Anal region not delimited from last substrate segment which still has setae and nephropores.
5	85/86	7	Anal region not delimited from last substrate segment where some of the setae still are present.
6	87/88	10	Anal region not delimited.

Time allowed for regeneration, 19 days.

Discussion

Homomorphic tail regeneration does not necessarily follow immediately after amputation and may not begin until nine months later. The process gets under way in some earthworm species, regardless of time of amputation, only when the "internal environment" permits. Differences in that environment may well be responsible for discordant results obtained by different investigators who have used the same species. As the importance of the unknown factors of the internal environment of earthworms seems not to have been appreciated, the following instance is worthy of record.

Individuals of *Eisenia foetida*, in the author's earlier studies (Gates, 1949-1950), after removal of the posterior portion at

levels behind 40/41, almost always regenerated promptly and in all seasons of the year. Several dozen specimens of that species, apparently in good condition, from three localities, were deprived of their tails in the region between 40/41 and 50/51 on three occasions in the last five years, to provide material for a school demonstration. All of the worms survived the operation. Not one showed any indication of formation of new segments during a period of several weeks though the external environment was, so far as could be determined, the same as before.

Summary

Cephalic regeneration in an anterior direction can be expected, in *D. rubida* in optimal conditions, at all levels back to 17/18, with equimery back to 5/6. Caudal regeneration in a posterior direction, from a growth zone of rapid segment formation, cannot be expected ordinarily if at all. Instead, the terminal substrate segment may be reorganized into an anal region and one or two metameres with some of the stigmata of regeneration, the reorganization possibly being more drastic and more rapid when at more anterior levels.

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